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THE

DEVELOPMENT AND ANATOMY OF

SARRACENIA PURPUREA L.

by

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THE DEVELOPMENT AND ANATOMY OF SARRACENIA PURPUREA L.

The earliest mention of _Sarracenia purpurea_ in botanical literature is made by De L'Ecluse in his Rariorum Plantarum Historia. This work has been accessible to me only in the edition of 1601, and whether or not Sarracenia is mentioned in the first edition of 1576 I am unable to state. De L'Ecluse saw only the vegetative parts and these in the dried condition, yet he has given a good description and a very faithful wood-cut of the plant, to which he gave the name _Limonium peregrinum_. He seems to have been impressed with the remarkable structure of the leaves of Sarracenia, but knew nothing of its home or habitat.

A more complete description was given by Robert Morison in his Plantarum Historiae Universalis in 1699, the plant being designated by him _Coilophyllum Virginianum breviore folio, flore purpurascente_. Along with this

was described *Coilophyllum Virginianum longiore folio erecto, flore luteolo* which is beyond doubt *Sarracenia flava*. These plants were sent to Morison from "Virginia" by J. Banister, who had seen them growing. Morison was the first to describe the flower of *Sarracenia*, which he does accurately although not very fully. Of the remarkable style he says: "Fructus in apicem prodigiosum definit, qui ubi semiuncialem longitudinem acquiserit in latum pentagonum quasi florem monopetalum binas pene uncias latum, se expandit, et operculi arcuati, umbellae aut canopaei forma, quod vasculo ab aeris injuriis defendendo idoneum est, vicem praestat."

The present generic name of Sarracenia dates from Tournefort's Elemens de Botanique (1797). In honor of a physician of the name Sarazin, who had sent him specimens of the pitcher-plant from Canada, Tournefort named it Sarracena.

The development of knowledge of the physiological habit of *Sarracenia* may be dated from William Bartram's

volume of "Travels through North and South Carolina" published at Philadelphia in 1791. In describing Sarracenia flava and mentioning the occurence of water in the pitchers he says: "these latent waters undoubtedly contribute to the support and refreshment of the plant, - - - but whether the insects caught in their leaves, and which dissolve and mix with the fluid, serve for aliment or support to these kind of plants, is doubtful. All the Sarracenias are insect catchers and so is the Drosera rotundifolia."

The work of Goebel (1893) has placed the Sarracenias in that class of insectivorous plants which are without a digestive enzyme in the water of their pitchers, although unpublished work by Gies throws doubt upon this view.

SYSTEMATIC POSITION OF THE GENUS AND FAMILY.

Sarracenia purpurea is a form presenting but little variability, and sharply distinct from the other members of the genus, although hybridizing readily with several

of them. The family Sarraceniaceae is a natural one, yet one of which the relationships and systematic position have been in controversy. The first author to give the genus Sarracenia a definite position in the natural system was Link, who in 1822 placed it in the Papaveraceae. The family Sarraceniaceae was established by La Pylaie in 1827, being constituted at that time of the genus Sarracenia alone. Heliamphora nutans, discovered by Schomburgk in British Guiana and described by Bentham in 1836 was referred to the Sarraceniaceae, as was also Darlingtonia californica, found in California by Brackenridge and described by Torrey in 1854. These three genera, Sarracenia with seven species, the others monotypic, now constitute the family.

Endlicher (1849), and Baillon (   ) have emphasized the relationship of the Sarraceniaceae to the Nymphaeaceae; Grisebach in 1854 placed the genus in the Droseraceae; Lindley in 1847 placed the family between the Papaveraceae and Ranunculaceae; and Bentham and Hooker, between the

Nymphaeaceae and Papaveraceae. Eichler in 1875 brought together the families Sarraceniaceae, Droseraceae, and Nepenthaceae, placing them between the Violaceae and Cistaceae in his group Cistiflorae. Engler (1891) has placed these three families together to form the series Sarraceniales, between the series Rhoeadales and Rosales, saying however: "wiewohl ich noch keineswegs von einer wirklich genetischen Verwandschaft der drei **F**amilien untereinander überzeugt bin." Macfarlane (1893) has united the Sarraceniaceae and Nepenthaceae to form a family, Ascidiaceae, largely on the ground of common features of leaf development in members of the two families.

GEOGRAPHICAL DISTRIBUTION.

The genus Sarracenia is endemic to Eastern North America, reaching its greatest development in the Gulf States, where all seven species are found. Sarracenia purpurea has by far the widest distribution of any member of the genus, ranging from De Funick Springs, Walton Co., Florida (Julia

Randall), along the Gulf of Mexico to Mobile Co. Alabama (Charles Mohr), and thence northward along the Atlantic coast, being most abundant (in collections at least) east of the Alleghany mountains. In the mountains it attains to an altitude of at least 550 metres (A. A. Heller). Along the Atlantic coast the range extends without break to the New England states, and from New Brunswick, Nova Scotia and Newfoundland to the coast of Labrador, where it has been collected in localities not definitely given (C. A. Kenaston; W. A. Stearns). The western boundary of its range reaches Clarke, Missouri (L. M. Umbach), Beltrami Co., Minnesota (Field Columbian Museum), and Prince Albert, Saskatchewan (Macoun). The last locality and Nelson, Hudson Bay (J. Fowler) are the most north-westerly stations from which the species has been collected.

The accompanying map indicates the localities represented by specimens in the following herbaria: Harvard University, Cambridge; New England Botanical Club, Boston;

New York Botanical Garden, New York; Academy of Sciences, Philadelphia; Herbarium of Capt. John Donnell Smith, Baltimore; National Herbarium, Washington; Herbarium of the Field Columbian Museum, Chicago; Herbarium of the Canadian Geological Survey, Ottawa.

The area of distribution of Sarracenia purpurea is apparently continuous. The greatest development of the species in number of individuals and their relative dominance among plants of the same habitat is in a belt of territory stretching from the Maratime Provinces of Canada westward to the north of the Great Lakes as has been shown by Transeau (1903) to be true of a number of characteristic bog plants. Nevertheless the presence of its congeners in the Gulf States would indicate that Sarracenia purpurea has had its origin in the south-eastern United States and has spread thence north-east and north-west, which Adams (1902) has suggested to have been the case with very many

species of plants and animals. The greater development of Sarracenia purpurea in the northern area may be accounted for by the greater frequency in that region of favorable habitats,- the sphagnum moors in which, as is well known, it occurs most frequently and thrives best.

MATERIAL; METHODS.

The work of which the results are here given was undertaken at the suggestion of Dr. D. S. Johnson, and has been carried out at the Biological Laboratory of the Johns Hopkins University. I wish here to express my thanks to Dr. Johnson for much advice and helpful criticism in connection with the work, and to express to Professor William K. Brooks my appreciation of his interest and encouragement. I also wish to thank my fellow-student Mr. Samuel Rittenhouse for his kindness in gathering material for me during my absence from the country in the spring of 1903.

The material worked upon has been obtained mainly at Glenburnie, Maryland, near Baltimore. Most of the material

was fixed in the field; of several killing reagents tried 1% chrom-acetic and Carnoy's mixture were the most satisfactory. Preparations were made by the ordinary parrafin method and stained with the Flemming triple or with cyanin and erythrosin.

GROSS ANATOMY.

The gross anatomy of *Sarracenia purpurea* has been sufficiently well made known by the descriptions of Tournefort, Morison and later systematic writers to require but brief review here. The plant consists of a rosette of leaves arising from the summit of a stout vertical rhizome. The leaves are all pitchered, showing no seasonal dimorphism as in *Sarracenia flava* and *Sarracenia drummondii*. Plants growing in situations which are shaded or drier than is the common habitat show a tendency to elongation of the leaf, a reduction in the diameter of the pitcher and a corresponding increased development of the wing. The

leaves lie prone upon the surrounding moss, and as the older ones decay and younger ones are developed the rhizome sinks into the bog by the weight of the water in the leaves. Adventitious roots arise, growing through the bases of the old leaves by which the rhizome is covered.

The leaves of Sarracenia purpurea persist throughout the winter, being sufficiently elastic to withstand the freezing of the water which they contain, and unless badly damaged through the perforation of the walls by insects, they function a second year. Each plant forms in the spring about five or six new leaves which, in the vicinity of Baltimore, begin to expand in the first or second week in April. In the young leaf, as will be noted later, the cover is folded together and the edges are united so as to close the pitcher. Not until the middle of May does the leaf

reach a size approaching that of maturity and open at the cover. There is no liquid in the pitcher at the time it opens save for a very few drops about the sides. After a few weeks the young pitchers are found to contain water, which I have no evidence for believing is other than rainwater.

GROSS STRUCTURE OF THE FLOWER.

The flowers of Sarracenia purpurea are axillary and borne singly, or in rare cases in twos, threes or greater numbers upon the plant. The scape begins its elongation in the first or second week of April according to the advancement ofthe season, and the buds are at first erect. When the scape has reached a length of from 2 to 3 dm., about two weeks after its elongation begins, the end is bent so as to deflect the axis of the bud a little below the horizontal. The scape of the mature flower is from 2.5 to 5 dm. in length.

The flower is perfect, hypogynous, and radially sym-

metrical. Three stout bracts envelop the bud during its winter rest and in the spring scarcely grow at all, forming a very inconspicuous part of the flower. The sepals are 5 in number, the petals 5 and the stamens from 70 to 80. The pistil is compound, the ovary being approximately spherical and surmounted by a style which is closely comparable to a raised umbrella (Fig. 30). The stalk of the style, corresponding to the handle of the umbrella, is about equal in length to the height of the ovary, and the upper spreading portion, which I shall designate as the umbrella, is so large as to cover the stamens completely. The stylar umbrella is roughly pentagonal in form (Fig. 29) and convex upward, bearing the five stigmatic surfaces on short papillae situated on the under surface of the umbrella a short way from the angles of the pentagon opposite the ends of notches in these angles (Fig. 30). The petals are inserted at the base of the ovary and curve up over the umbrella opposite the sides of the pentagon, having an inden-

tation just below the point where they curve over the umbrella... The points of the umbrella bearing the stigmatic papillae project between the petals. The sepals stand out more stiffly from the umbrella.

Cross-pollination is effected in Sarracenia purpurea by humble-bees, whch are apparently attracted by the secretions of the glandular surface of the ovary. The mechanism of pollination is as has been pointed out by Hildebrand (1882). The bee forces its way between the petals and in so doing must pass under the angle of the umbrella and brush its back, laden with pollen from the last flower visited, against the stigmatic surface. After pollination the petals and stamens fall, but the sepals and style persist until the maturity of the seed and dehiscence of the capsule.

DEVELOPMENT OF THE FLOWER.

The earliest stage observed in the development of the flower was in material gathered on the 30th of August. There are then to be seen the primordia of the three bracts, the

five sepals and the five petals, which have apparently arisen in the order named. The bracts and sepals are at this time imbricated, but the edges of the petals are separated by a space of approximately half their width. Lying just within the edges of the petals are the staminal primordia, as yet mere papillae, and within them is a flat surface with a slight elevation at the centre. A somewhat later stage than the last shows progress in the development of the stamens, which now appear as ten groups of protuberances lying in the position before noted (Fig. 2). Each group arises from a base which is distinct from the bases of the adjoining groups, and is made up of the primordia of from five to eight stamens. There is no suggestion of a pairing of the groups nor of their falling in two whorls. Upon the central flat surface has arisen the ovary, which at its base is pentagonal in outline and at its apex is surmounted at the angles of the pentagon by the tips of the carpellary

leaves. The outgrowths of the wall of the ovary which are destined to give rise to the placentae are upon the sides of the pentagon, which shows each placenta to be made up of the edges of two carpellary leaves (Fig. 2 and Fig. 14).

MICROSPORANGIUM AND MICROSPORE.

The staminal primordia early show differentiation into the parts destined to give rise to filament and anther. The latter portion bears approximately the same outline in cross-section as do the mature anthers. The location of the archesporium is indicated at first only by the slightly greater size of the nuclei in the region of the four microsporangia (Fig. 4), but soon comes to be more sharply defined by the concentric arrangement of cells in the region of the future parietal cells. The archesporium is at this earliest recognizable stage of about six cells in cross-section, but grows rapidly to a size of about twelve cells in diameter (Fig 5). Development proceeds in the autumn to the differentiation of the endothecium, the two to three parietal layers, and the pollen mother-cells. There is as yet no distinction

of definitive sporogenous cells and tapetum. In this condition the stamens pass the winter.

The elongated parietal cells do not contribute to the tapetum, but it is made up entirely from the isodiametric cells of the primary archesporium. The outer outline of the tapetal layer is continuous, and the inner is irregular only to an extent which makes it in some places two cells in thickness and in other places in the same cross-section, three. The cells of the tapetum do not wander among the definitive sporogenous cells. Shortly after the differentiation of the tapetum, and before the pollen mother-cells are in the synapsis stage, the the tapetal nuclei divide once by mitosis, and so far as observed once only. At the time of tetrad division the tapetal nuclei are enlarged, the chromatin is granular and scattered and the nucleoli are large. At the time of the formation of the walls of the pollen-grain the cytoplasm of the tapetal cells becomes much vacuolated and the nuclei lose their chromatin; but

at no time does the layer become broken. The parietal layers at the time of the tetrad division are from three to five in number, the endothecium is thickened on its inner and lateral walls and the epidermis is undifferentiated. The thickening of the endothecium walls takes place very late,-simultaneously with the division of the pollen-grain nucleus,-the cells for some time previous to this being filled with starch.

Dehiscence is by means of two longitudinal slits, each of which opens two pollen-sacs of the anther. A deep crease runs between each pair of pollen-sacs upon the two sides of the anther, penetrating to the point at which the two microsporangia lie nearest each other (Fig. 13). At this point is a group of small cells reaching from one microsporangium to the other, the walls of which are thrown into creases and folds, and fail to thicken in the further development of the anther, as do the neighboring cells.

The pollen mother-cells apparently lie in the synapsis

stage for several days. At their first division it is possible to count the chromosomes, the reduced number being twelve and their form short and blunt(Fig. 8).

The tetrahedral division is simultaneous, there being no formation of wall after the first division. After a short period of adherence in tetrads the pollen grains round off and acquire the coats,- the characteristic exine and intire. The mature pollen-grain is marked with eight meridional grooves in such a manner as to resemble a musk-melon. Beneath the grooves the intine is several times thicker than between the grooves (Fig. 11). While the pollen-grain is yet within the anther the nuclear division takes place which gives rise to tube and generative nuclei (Fig. 12). In this condition the grains are shed, the stamens nearest the ovary opening first, and the outer ones successively.

OVULE AND MEGASPORANGIUM.

The placental outgrowths which we have seen to arise

from the flat sides of the ovary, at the point of juncture of the edges of the carpellary leaves, grow inward almost to the centre of the ovary, and these I shall designate as the "main placental outgrowths" (Fig. 14). Each main placental outgrowth sends out two lateral outgrowths so as to resemble in cross-section a letter T in which the arms have been bent downward. Each pair of adjoining lateral outgrowths is closely appressed and directed backward toward the angles of the ovary. In the lower part of the ovary the adjacent lateral outgrowths fuse, but do not extend to the bottom, and in the upper part they do not reach the wall of the ovary as do the main placental outgrowths. Upon the edges of the lateral outgrowths are borne the ovules (Fig. 15). The ovules at the base and top of the ovary lie parallel to the axis of the flower, those in the middle lie at right angles to it, the intermediate ones having intermediate positions according to their place in the ovary.

The summits of the carpellary leaves broaden and coalesce, and grow out in a direction radial to the axis of the flower, so that while their basal parts form the capsule and the stalk of the style the tips form the umbrella of the style (Fig. 3). The tip of each carpellary leaf organizes a very definite growing-point (Fig. 23), and the portion between the tips nearly keeps pace in growth. Upon the ventral surface of each tip near the time of the completion of ~~the time of~~ its growth is formed the protuberance which bears the stigmatic surface.

The appearance of the primordia of the ovules upon the placentae takes place from the point opposite the angle of the ovary wall, where the adjacent lateral outgrowths meet, successively toward the angle formed by the lateral outgrowth and the main outgrowth (Fig. 19). In a vertical direction the development proceeds from the middle of the placenta toward top and bottom. The ovules first appear as pro-

tuberances initiated by the periclinal division of subepidermal cells and the accompanying anticlinal division of the epidermal cells, as is commonly the case. When the ovule first protrudes from the placenta there is no suggestion of a sporogenous cell. At this stage of development the winter rest intervenes. The first suggestion of a sporogenous cell comes with the enlargement of a single subepidermal cell, which is the megaspore mother-cell (Fig. 16). In three cases out of many hundreds examined there were two megaspore mother-cells lying side by side. There is no tapetal cell.

The bending by which the ovule becomes anatropous begins at once and is quite marked by the time of the appearance of the megaspore mother-cell. Both transverse and longitudinal sections (Fig. 16 and Fig. 17) show a double layer of cells at the sides of the megaspore mother-cell, and median longitudinal sections show approximately five rows of cells in the ovule, exclusive of the epidermis.

The integument is single in Sarracenia purpurea. Its development begins by periclinal divisions of subepidermal cells upon the convex side of the bending ovule, and continues as a ring which grows rapidly on the side where it began first and slowly on the opposite side, which lies next the raphe. The rapid growth of the ovule is accomplished by the chalazal end. By the time of the first division of the megaspore mother-cell the bending of the ovule is completed, the integument has grown so as to nearly close the micropyle and the megaspore mother-cell has increased in size and encroached upon the nucellar tissue so as to lie next the epidermal cells over the entire distal end (Fig. 20).

The difference in the time of appearance of the ovules upon the different parts of the placenta causes a difference in the degree to which the integuments develop (Fig. 19) and also a difference in the maturation of the megaspore mother-cell, and the germination of the megaspore in ovules in

the different parts of the placenta, a difference which long remains evident, as will be noted later.

At the first division of the megaspore mother-cell it was not found possible to count the number of chromosomes. The division is followed by the formation of a wall (Fig. 20), and in about half the cases observed both the daughter cells again divide to form the normal tetrad of megaspores arranged in linear series (Fig. 23). In the remaining cases the micropylar daughter cell fails to divide, resulting in a series of three megaspores (Fig. 21); and and much less frequently the micropylar daughter cell divides ~~transversely~~ longitudinally to the long axis of the nucellus (Fig. 22). In any case it is the chalazal megaspore which functions, the micropylar ones, be they three or two being appressed to the layer of the nucellus and absorbed.

The maturation of the megaspore is concident with the tetrad division of the microspore mother-cells.

EMBRYO-SAC.

Such has been the elongation of the ovule by the time of the maturation of the megaspore that the nucellus is lengthened to five or six times its diameter, being made up of slightly elongated cells from five to six rows thick in median section. The integument, about five cells thick, has now grown well beyond the tip of the nucellus and its lips have become somewhat appressed to form the long micropyle. The cells in the innermost layer in the integument show active division in the direction of the greatest length of the nucellus, and by their dense protoplasm and large nuclei stand out prominently as a definite layer which I shall designate as the "columnar tissue."

After the disappearance of the megaspore sister-cells the definitive megaspore continues its absorptive activity to the destruction of the single layer of nucellus at its micropylar end (Fig. 23), so that the distal half of it comes to lie directly against the columnar tissue of the integument.

The chalazal end is pointed, occupies at this time a median position in the nucellus, and is apparently active in the degeneration of the nucellar tissue, in accomodation to its own growth. About this time the definitive megaspore undergoes division. The daughter nuclei take places at opposite ends of the embryo-sac (Fig. 24), and quickly undergo the second (Fig. 25) and third divisions in the normal manner.

The mature embryo-sac is typical in every respect. It is elongated to four or five times its width, the sides lie next the columnar tissue and the base continues to be pointed and median. The synergidae lie side by side and the egg protrudes a little way below them, nearer the centre of the sac. The cytoplasm of the synergidae is dense and stains heavily with the Flemming triple; That of the egg is greatly vacuolated. The antipodals lie well together in the conical base of the sac (Fig. 26). The polar nuclei meet midway between the ends of the sac, and after their

fusion the endosperm nucleus continues to occupy this position (Fig. 26). After the fusion of the polar nuclei the endosperm becomes very active in the disorganization of the remaining basal portion of the nucellus. In this activity the antipodals do not take part. The base of the sac remains pointed, but from being median now comes to lie against the columnar tissue at one side of the nucellus by means of the absorption of the nucellar tissue which lay between its previous position and the columnar tissue. The further enlargement of the sac is accompanied by a pushing downward of the base between the nucellus and the columnar tissue, and in some preparations the antipodals would seem to have been pushed to one side (Fig. 27). The columnar layer now shows its maximum development, being made up of deep much-flattened cells with darkly staining cytoplasm. The function of these cells is no doubt that of secreting and passing over to the sac, sugars or other elaborated food-stuffs.

POLLINATION AND POLLEN-TUBES.

Pollination takes place, near Baltimore, in the first week in May. In the mature style of Sarracenia at the time of pollination the umbrella is of a pale green color. Its internal structure is leaf-like, without a definite palisade, but with abundant intercellular spaces and stomata numerous upon the upper surface and few upon the lower. Long unbranched unicellular hairs cover the lower surface so thickly as to form a tomentum in which considerable pollen is caught at the time of its shedding. There are also upon both sides of the umbrella multicellular glands of spheroidal shape projecting slightly above the level of the epidermis. Running from the five stigmatic surfaces toward the centre of the umbrella are heavy veins which comprise both vascular and conducting tissue.

The union of the carpels in the formation of the stalk of the style is such as to leave at its centre a pentagonal cavity which in the mature flower connects the interior of the capsule with the external air. An examination of the veins

of the umbrella two weeks before pollination will show the conducting tissue as a cylindrical strand about ten cells in diameter. The cells are much elongated, with pointed ends, or many cells of this description have divided to two or four cells. The cytoplasm is dense, the nuclei are large, elongated, often three times as wide as long, binucleolate and poor in chromatin. At the time of the passage of the pollen-tubes the conducting strand has become enlarged to more than twice its previous diameter at the expense of the surrounding tissue, and the cells have become still more elongated. The cytoplasm is much vacuolated, and the nuclei are attenuate at the ends and devoid of nucleoli (Fig. 32 and Fig. 33), and there are large intercellular spaces. The vascular tissue of the veins lies beneath the conducting tissue and is continuous with the vascular tissue of the stylar stalk.

Two weeks before pollination transverse sections of the stalk of the style will reveal five strands of heavy-

walled cells running from the angles of the central cavity half way to the periphery (Fig. 34). The tissue which these cells represent in cross-section is four to six cells thick and runs the entire length of the stalk, being in the median line of the carpels. About the time of pollination these sheets of cells are found to split to two layers which separate in such a manner as to form canals which are connected with the central cavity (Fig. 35). The surface layer of cells on the interior of the canal becomes detached and undergoes partial degeneration. The five conducting canals thus formed are continuous with the conducting tissue of the veins of the umbrella above, and open below midway between the main placental outgrowths.

The stigmatic surface is richly provided with long, curved, heavy-walled outgrowths of epidermal cells (Fig. 31), which serve to catch pollen and hold it. Pollen was found to be present in abundance on all stigmas examined. There is no definite sprouting pore in the grains but the tubes

grow more commonly from the meridional grooves. The pollen-tubes grow between the cells of the stigmatic surface and their entire passage is between the cells of the conducting tissue and never through them. They follow the well-defined course of the conducting tissue along the vein of the umbrella and down the stalk of the style.

The generative nucleus was not seen in any case to have divided before the sprouting of the pollen-tube and the earliest position in which it was seen to have divided was in a tube which had nearly reached the centre of the umbrella. The tube nucleus is spherical and precedes the generative nuclei. The latter are alike in form,- elongated and curved or often bent twice in serpentine manner. The distance of the nuclei from the end of the tube is from four to six times the diameter of the tube. The cytoplasm is dense in the entire end and around the nuclei (Fig. 36).

When the pollen-tubes enter the cavity of the ovary from the five conducting tubes of the stalk they are directly above the line of junctureof the two adjacent lateral

placental outgrowths. The course of the pollen-tubes is at first a downward one between these outgrowths , and later an outward one radial to the axis of the ovary (Fig. 30). In this manner the edges of the placentae are reached after a course which, for the tubes growing to the lowermost ovules, is as much as 6 or 8 mm. and lies entirely outside the tissue of the plant in an ovary the cavity of which has, as already said, direct communication with the external air. The epidermal cells of the placental surfaces between which the pollen-tubes pass are densely filled with cytoplasm; beneath them lie three layers of flattened cells of similar contents.

Thin transverse walls are formed in the tubes near the stigmatic surface (Fig. 37), and far down in the ovary near the ovules plugs are not infrequent in the tubes, being from three to six times the diameter of the tube in length.

The distance traversed by the pollen-tubes which reach the lowermost ovules is, in flowers of average size,

about 4 cm. Provision for the nutrition of the tube during its growth and passage is perhaps made in part by the photosynthetic activity of the umbrella. Previous to pollination the epidermal, subepidermal and some deeper cells of the umbrella are filled with densely-staining, finely granular contents, the nature of which has not been determined. Similar contents fill the epidermal cells of the stalk of the style. The course of the tubes as far as their entrance to the ovary is undoubtedly through a strong solution of sugars. Below the point of entrance to the ovary the passage between the placental walls is probably through a film of sugary solution held there by capillarity and supplied with materials from the epidermal cells of the placental walls, which after pollination are highly vacuolated, in marked contrast to their condition before pollination.

FERTILIZATION.

The fusion of the male and female nuclei in fertilization is preceded by the division of the endosperm nucleus in

nearly all the embryo-sacs. Fertilization takes place in all ovules at nearly the same time without regard as to whether the endosperm nucleus has or has not divided. As to the length of time intervening between pollination and fertilization I am unable to give any exact data. On the 24th of May plants growing in the open were found to have shed their pollen in the anthers nearest the ovary. Material collected at the same localuty two days later was found to show fertilization. The time of pollination of the particular flowers gathered and fixed may have been as much as five days before gathering, but was probably not earlier.

The thin-walled slender pollen-tubes may be found in abundance about the mouths of the micropyles often forming considerable knotted masses. The cells which line the micropyle are heavy-walled and of such darkly staining contents that it is difficult to observe the pollen-tube with-

in the micropyle, and indeed the entrance of the tip of the tube, with the nuclei, was not observed. The synergidae become appressed to the wall of the sac. The end of the tube upon entrance to the sac becomes expanded and pushes downward to one side of the egg. The generative nuclei have lost the elongated shape they were seen to have while passing down the style and have become spherical. Fusion of the first generative nucleus takes place in a manner presenting no special peculiarities (Fig. 38).

ENDOSPERM.

The fusion of the polar nuclei precedes fertilization, as has been noted, and is followed at once by division. The first wall in the endosperm is transverse to the length of the sac and divides it into equal halves (Fig. 39). The daughter nuclei divide in like manner (Fig. 40), as do also the grand-daughter nuclei, giving rise to an endosperm of eight cells in linear series, in which the walls are all

transverse, although not uncommonly somewhat oblique (Fig. 41) Subsequent divisions are less regular, and by the time the fertilized egg has divided to a two-celled embryo the endosperm contains approximately 150 cells, its base having used up the nucellus either competely or to the extent of all but a half dozen cells (Fig. 42). At this time the endosperm cells are highly vacuolated and the laying down of food has not begun.

The relative rate of development of the endosperm in ovules upon different parts of the same placenta is the same as was noted with regard to the integuments. An ovule at the point of juncture of the adjacent lateral placental outgrowths may have an eight-celled endosperm at the same time that the endosperm nucleus has not yet divided in an ovule upon the edge of the placenta nearest the main placental outgrowth.

EMBRYO.

The first division of the fertilized egg is in a direction parallel with the length of the sac. The two-celled embryo (Fig. 43) at first oval becomes gradually elongated, divisions following in the same plane as the first but not in a manner in which it has been possible to discover any regularity. After the embryo has attained to a length of from five to seven cells there is a lateral division of the terminal cell (Fig. 44), the beginning of the embryo proper. The suspensor is usually curved, although not always to so great an extent as shown in the figure. I have been unable, by lack of material, to observe stages in the development of the embryo immediately following the transverse division of the terminal cell.

In material of the 25th of June the embryo proper is found to have reached a size of approximately 250 cells, with ellipsoidal form (Fig. 45). Dermatogen and periblem are well defined but no procambial cells have as yet ap-

peared. The endosperm has by this time increased greatly in diameter, encroaching upon the tissue of the integuments. The endosperm cells have become well stored with aleurone except in the central portion of the micropylar end,- the region destined to be occupied by the full-sized embryo of the mature seed. In embryos of the size of that shown in Fig. 45 the suspensor is surrounded by endosperm cells in which the aleurone has been laid down; the embryo proper is surrounded by cells of highly vacuolated contents.

SEED AND SEEDLING.

Material gathered during the last week of July exhibits seeds which are practically mature. The embryo-sac has grown to an elongated ellipsoidal form, the cotyledons being about one third of the length of the whole (Fig. 46). Elongated procambium cells stretch from the basal end of the embryo to the region of the stem growing-point. Stomata are not formed in the embryo until the time of germination. A few endosperm cells at the sides and cotyledonary end of the

embryo are free of aleurone, as they remain in the mature seed.

The superficial layer of the integument forms the seed-coat. Its cells become irregular on their external surface and the walls are greatly thickened, with conspicuous pores in the lateral and basal walls, but none in the walls forming the surface of the seed (Fig. 47). The inner cells of the integument are all disorganized by the growth of the endosperm and reduced to a layer of the remaining walls of flattened cells. The raphe of the ovule develops into a wing upon one side of the seed as seen in Fig. 47. In the mature seed there is a coating of wax upon the surface which renders them unwettable, a condition in which they remain for several weeks after they have been placed in wet moss.

Provision for the shedding of the seed is made by a deep furrow surrounding the raphe just at its junction with the placenta (Fig. 48). The dehiscence of the capsule is loculicidal, and is provided for by a deep suture upon

the external surface of the capsule wall at a point where the wall is traversed by a heavy vascular bundle. Dehiscence takes place late in September or early in October, the seeds are scattered gradually during many weeks by chance shaking of the scape by wind or animals. The old flower, with stigma and sepals still persisting, is often found side by side with the bloom of the following year.

On germination the seed is elevated above the soil or moss by growth of the hypocotyl, which is sharply bent and is the first part of the seedling to protrude. The tips of the cotyledons remain for some time in the seed, functioning as haustoria for the removal of the stored food of the endosperm. The tips of the cotyledons are active in the removal of the endosperm both at their ends and along their sides (Fig. 49). The cotyledons expand to ligulate leaves about 1 cm. long (Fig. 50) and persist until about the time of the formation of the third epicotyledonary leaf. The cotyledons develop stomata during the process of germin-

ation and the epidermal and subepidermal layers of isodiametric cells bear chlorophyll.

DEVELOPMENT OF LEAVES.

The stem growing-point of Sarracenia is massive and acutely dome-shaped in the seedling (Fig. 51). There is a definite layer of dermatogen and a common group of initials for periblem and plerome. The first epicotyledonary leaf arises opposite the interval between the cotyledons. It is finger-shaped with a somewhat broadened base. On reaching a length of about twice its diameter there begins a rapid lateral outgrowth of the tissue of an O-shaped area on the side of the primordium which faces the growing-point, giving rise to a pit which is destined to become the cavity of the pitchered leaf (Fig. 52). The basal part of the O-shaped outgrowth now begins to grow upward, in which it is accompanied at the same rate by the upper portion of the O, which at the same time carries forward the apical

growth of the leaf (fig. 55). The cavity of the pitcher thus grows in depth by the upward growth of the tissue by which it is surrounded. The bottom of the cavity is subsequently elevated to some extent by the further growth of the tissue beneath it, but there is no depression, which was considered as a possibility by Zipperer. The entire early development of the leaf resembles closely that which has been described for Darlingtonia californica by Goebel (1893).

The first epicotyledonary leaf reaches its maximum size at a length of about 2.5 cm., it is slender in form, the cavity reaches well down toward its base, and the wing is but slightly developed. At the summit it is hooded in such a manner as to resemble the mature leaf of Sarracenia variolaris. The walls of the pitchers of the seedling are six to eight cells in thickness, with open mesophyll, chlorophyll in all the cells, and stomata over the entire external epidermis. There are two principal strands of vascular tissue, one in the base of the wing and one on the

opposite side of the pitcher from this, with smaller anastomosing strands between these. In the throat of the pitcher all the epidermal cells are produced into long projecting points; lower in the pitcher occasional epidermal cells, smaller than the others, give rise to long heavy-walled hairs, while in the bottom of the pitcher the epidermal and first layer of subepidermal cells are small and heavy-walled.

While each leaf of the young plant is passing through its period of most active growth, the internode between it and the next lower leaf is also elongating rapidly. A young leaf appears for this reason to arise from the petiole of the leaf below it (Fig. 51). The relative elongation of the internodes is far greater in the seedling than in the adult plant.

The growth of a single plant from seedling to adult has not been followed by the writer, but the available evidence points to the time requisite for the seedling to reach blooming age, as being at least five or six years.

Seeds of the crop of 1901, which in October of that year were placed in sphagnum in a loosely covered glass vessel, germinated in July 1902, and now, after 33 months, have no pitchers measuring over 2 mm. in diameter. The extremely artificial conditions under which these seedlings were kept would however make it inadvisable to draw from them any general conclusions as to the rate of growth in the seedlings under natural conditions. The great number of intermediate stages in growth between the seedling and adult which may be observed in a single locality at any one season, would also argue for the slowness of the plant ~~to~~ in reaching adult size.

The stem growing-point of the adult plant is more broadly dome-shaped than that of the seedling but is identical with it in the mode of origin of the dermatogen, periblem and plerome. The earliest primordium of the leaf is likewise more massive than in the seedling but essentially similar. Its form is conical, with a broadly semicircular base embracing the growing-point. Near the summit, upon

the side toward the growing-point is developed the narrow pit which is destined to form the cavity of the pitcher, its origin being due wholly to a difference in the rate of growth of the tissue at the bottom of the pit and that forming its sides (Fig. 54). Baillon (1871) in a brief note on the development of the leaf of a Sarracenia (species not mentioned) has described this early stage and called attention to its similarity to an early stage in the development of peltate leaves, averring that "La membrane qui tapisse intérieurment l’urne n’est autre chose que l’epiderme supérieur de la feuille." This may be an entirely superficial analogy or it may be a hint as to the ultimate origin of such a markedly modified leaf. Goebel (1893) has figured the early leaf primordium of *Sarracenia drummondii* which is essentially like that of *Sarracenia purpurea*.

With the continued growth of the leaf rudiment the pit becomes deeper, and its mouth becomes vertically elongated although remaining very narrow. At stages somewhat

earlier than that shown in Fig. 55 the sides of the mouth of the pit will be found to have come together, closing the pit completely. Fig. 55 represents a leaf primordium in which the wing is just beginning to appear. Figs. 56, 57, 58, 59, 60 and 61 represent cross-sections of the primordium at this age in the places indicated in Fig. 55.

In older leaves such as are represented in Fig. 62 the base of the leaf primordium is of a stoutly crescentic form in cross-section. Through the groove at the inner side of the leaf base the next younger leaf appears (Fig. 55 and Fig. 62). The groove becomes narrower and more shallow as we pass up the leaf and ends just short of the bottom of the cavity of the pitcher (Fig. 62). Above the end of the groove there is a short portion of the young leaf which is circular in cross-section, above which in turn the narrow flattened outgrowth of the wing has become more conspicuous. The wing rudiment ends rather abruptly at a point where retardation of growth in diameter indicates the line of de-

marcation between the pitcher and cover. The cavity of the pitcher at this stage of development reaches as far as the upper end of the circular portion of the base.

There have been many suggestions as to the homology of the parts of the pitchered leaf of Sarracenia. A view held by many workers is that the pitchered portion of the leaf is derived from the primordium of the petiole and the cover from the primordium of the lamina. Goebel (1893) points out that since there can be no distinction in the very young leaf of primordia of petiole and lamina there can be no line drawn as to what portions of the pitchered leaf "represent" these structures.

The anatomy of the mature leaf was first worked out by Vogl (1864); it has more recently been reviewed by Goebel (1893) and minor contributions have been made by Schimper (1882) and Zipperer (1885). The leaves have a two-fifths arrangement subject to some irregularity. The first leaf rudiments unfolded in the spring are aborted

(Fig. 62), consisting of the sheathing base surmounted by the minute retarded primordium of pitcher and cover. These are usually three in number and may occur in plants which do not bloom,as well as in those which do. In the latter case the aborted leaves are those just above the one to which the flower is axillary.

The axillary buds of Sarracenia are commonly very small and constituted of growing-point and the primordium of a single leaf, completely covered and protected by the sheathing leaf-base. An occasional axillary bud develops, the first two leaves being opposite and on the opposite sides of a line connecting the growing-point of the bud with the centre of the shoot. There is thus brought about a branching of the rhizome, which by frequent repetition gives rise to large clusters of individuals.

The anatomy of the rhizome of *Sarracenia purpurea* has been described by Zipperer in sufficient detail, since it presents no unusual features. He has also

given a correct account of the growing-point of the root and the development of the vascular tissue of the root: the growing-point being of the type in which the cap and three tissue layers are all derived from a common group of initials, the early order of vascular bundles being triarch.

Root-hairs are few upon the roots of plants growing in a saturated substratum in the open, but are abundant in seedlings grown in highly saturated sphagnum, and in adult plants in the open which are growing in a substratum merely moist. Mycorrhiza has not been observed in Sarracenia purpurea in the vicinity of Baltimore, although fungal threads have been found covering the root of seedlings grown under the conditions previously mentioned and penetrating the epidermis. MacDougal (1899) has described penetration of the epidermis by hyphae in adult plants without committing himself as to their mycorrhizal nature.

SUMMARY.

1. The flowers of *Sarracenia purpurea* are axillary, perfect, hypogynous and radially symmetrical.

2. The 70 to 80 stamens arise in ten groups.

3. There are four microsporangia. There is a double layer of binucleate tapetal cells, derived from the primary archesporium. There are from three to five parietal layers.

4. The tetrad division is simultaneous; the microspore nucleus divides before the dehiscence of the anthers.

5. The reduced number of chromosomes is twelve.

6. In the ovule there is a single archesporial cell, which is the megaspore mother-cell. There is no tapetal cell.

7. The ovule is anatropous and there is a single integument.

8. The megaspore mother-cell divides to a linear series of four megaspores, or after the first division the micropylar nucleus may fail to divide or may divide longitudinally.

9. The chalazal megaspore is functional, and develops a typical eight-celled embryo-sac.

10. The polar nuclei fuse and the endosperm may become two- to eight-celled before the complete fusion of male and female nuclei in fertilization.

11. The pollen-tubes grow through a definite conducting tissue in the upper expanded portion of the style, through schizogenic canals in the stalk of the style and between the placental outgrowths in the ovary.

12. The generative nucleus divides before the tube has passed into the stalk of the ovary.

13. Fertilization presents no peculiarities.

14. The embryo is elongated and straight, with cotyledons. The storage tissue is endosperm filled with aleurone. The seed-coat is the external layer of the integument.

15. The cotyledons function as haustoria in germination and survive as chlorophyll-bearing leaves.

16. The first epicotyledonary leaf is pitchered and arises from a finger-like primordium in which a cavity is developed by unequal growth.

17. The development of the leaves of adult plants is similar to that in seedlings.

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EXPLANATION OF PLATES I, II, III.

Abbreviations used: *ant*, antipodal; *arsp*, archesporium; *br*, bract; *cav*, cavity; *col* *t*, columnar tissue; *con* *c*, conducting canal; *con* *s*, conducting strand; *con* *t*, conducting tissue; *cot*, cotyledons; *cov*, cover; *cp*, carpel; *der*, dermatogen; *d* *s*, dehiscing slit; *e*, egg; *em*, embryo; *en* *n*, endosperm nucleus; *e* *s*, embryo-sac; *esp*, endosperm; *f* *n*, female nucleus; *g* *n*, generative nucleus; *int*, integument; *int* *i*, integument initials; l, leaf, *l* *p* *c*, lateral placental outgrowth; *meg* *mc*, megaspore mother-cell; *meg* *sc*, megaspore sister-cell; *mic* *mc*, microspore mother-cell; *micsp*, microsporangium; *mn*, male nucleus; *m* *p* *o*, main placental outgrowth; *nuc*, nucellus; *ov*, ovary; *par* *c*, parietal cells; *pet*, petals; *pn*, polar nuclei; *ppi*, initials of periblem and plerome; *pro* *c*, procambium cells; *pt*, petal; *sc*, seed-coat; *sep*, sepal; *st*, stamen; *stg* *s*, stigmatic surface; *stk*, stalk of style; *sus*, suspensor; *syn*, synergid; *tap* *c*, tapetal cells; *tn*, tube nucleus; *um*, umbrella of the style; *w*, wing.

All figures are camera drawings from microtome sections except figs. 29, 30, 50, 55 and 62, which are from free-hand drawings.

PLATE I.

Fig. 1. Vertical section of young flower bud. x 30.

Fig. 2. Transverse section of young flower bud of same age as in fig. 1. Dotted outline represents position of carpel tips in higher sections. x 30.

Fig. 3. Vertical section of older flower bud. x 30.

Fig. 4. Transverse section of young stamen. x 232.

Fig. 5. Transverse section of single microsporangium of older stamen. x 232.

Fig. 6. Transverse section of portion of microsporangium and wall in microspore mother-cell stage. x 400.

Fig. 7. Transverse section of portion of microsporangium and ~~portion of~~ wall with microspore mother-cells in synapsis. x 232.

Fig. 8. Transverse section of microsporangium and portion of wall. Pollen mother-cells in mitosis. x 400.

Fig. 9. Pollen mother-cells in metaphase of first mitosis.

x 400.

Fig. 10. Tetrads of microspores. x 400.

Fig. 11. Pollen-grain. x 400.

Fig. 12. Pollen-grain after division of nucleus. x 400.

Fig. 13. Transverse section of mature anther. x 20.

Fig. 14. Transverse section of young ovary. x 20.

Fig. 15. Transverse section through middle of nearly mature ovary. x 7.

Fig. 16. Longitudinal section of ovule with megaspore mother-cell. x 400.

Fig. 17. Transverse section of ovule through megaspore mother-cell. x 400.

Fig. 18. Longitudinal section of ovule with megaspore mother-cell and integument. x 232.

Fig. 19. Transverse section of single lateral placental outgrowth, showing difference in rate of development of integuments on different parts of the placenta. Somewhat diagrammatic. x 40.

PLATE II.

Fig. 20. First maturation division of megaspore mother-

cell. x 400.

Fig. 21. Linear series of three megaspores, arising by failure of micropylar daughter-cell to divide. x 400.

Fig. 22. Tetrad of megaspores in which the micropylar daughter-cell has divided longitudinally. x 400.

Fig. 23 Longitudinal section of ovule, with tetrad of megaspores, chalazal one enlarging and encroaching on single layer of nucellus. x 120.

Fig. 24. Longitudinal section of portion of ovule showing two-celled embryo-sac, nucellus and columnar tissue. x 232.

Fig. 25. Longitudinal section of portion of ovule showing four-celled embryo-sac. x 232.

Fig. 26. Longitudinal section of portion of ovule showing fully developed embryo-sac. x 400.

Fig. 27. Longitudinal section of portion of ovule showing embryo-sac after fusion of polar nuclei. Antipodals pushed to one side. x 232.

Fig. 28. Growing-point of tip of carpel in umbrella, horizontal section. x 40.

Fig. 29. Stylar umbrella viewed from above. In outline. x 2/3.

Fig. 30. Ovary and style to show course of pollen tube, indicated by dotted line. Somewhat diagrammatic. x 2.

Fig. 31. Longitudinal section of stigmatic surface with sprouting pollen-grains. x 120.

Fig. 32. Longitudinal section of conducting strand in umbrella of style, showing conducting and vascular tissue. x 40.

Fig. 33. Transverse section of upper surface of umbrella of style, showing conducting and vascular tissue and glandular epidermis. x 120.

Fig. 34. Transverse section of stalk of style before pollination. x 20.

Fig. 35. Transverse section of stalk of style at time of pollination. x 20.

Fig. 36. Tip of pollen-tube, from conducting tissue of umbrella. Optical section. x 400.

Fig. 37. Cross wall in tube near stigmatic surface. x 400.

PLATE III.

Fig. 38. Longitudinal section of upper end of embryo-sac showing fusion of male and female nuclei. x 400.

Fig. 39. Longitudinal section of embryo-sac showing two-celled endosperm, columnar tissue and remains of nucellus. x 120.

Fig. 40. Longitudinal section of embryo-sac showing four-celled endosperm. x 120.

Fig. 41. Longitudinal section of portion of ovule showing eight-celled endosperm and integument. x 40.

Fig. 42. Longitudinal section of seed through the wing showing multicellular endosperm and two-celled embryo. x 20.

Fig. 43. Two-celled embryo. x 232.

Fig. 44. Young embryo with suspensor. x 400.

Fig. 45. Older embryo with suspensor. x 232.

Fig. 46. Longitudinal section of embryo from mature seed. x 120.

Fig. 47. Transverse section of mature seed cutting the

embryo through the cotyledons. x 4[illegible].

Fig. 48. Longitudinal section through the hilum of nearly mature seed. x 120.

Fig 49. Longitudinal section of germinating seed, with cotyledons. Seed-coat has been removed. Portion beyond the dotted line is that from which aleurone has not yet been removed. x 20.

Fig. 50. Seedling with cotyledons and three epicotyledonary leaves. x 1½.

Fig. 51. Vertical section through growing-point of seedling. x 232.

Fig. 52. Median vertical section through primordium of first epicotyledonary leaf. x 232.

Fig. 53. Median vertical section through portion of primordium of first epicotyledonary leaf in later stage of development. x 232.

Fig. 54. Vertical section through growing-point and young leaves in adult plant. x 90.

Fig. 55. Surface view of primordium of leaf seen from the side, next younger leaf also showing. Dotted outline marks cavity of leaf. x 3.

Fig. 56. Transverse section of leaf in *fig.* *55* at 56. x 20.

Fig. 57. Transverse section of leaf in *fig.* *55* at 57. x 20.

Fig. 58. Transverse section of leaf in *fig.* *55* at 58. x 20.

Fig. 59. Transverse section of leaf in *fig.* *55* at 59. x 20.

Fig. 60. Transverse section of leaf in *fig.* *55* at 60. x 20.

Fig. 61. Transverse section of leaf in *fig.* *55* at 61. x 20.

Fig. 62. Later stages of young leaves. Cavities in dotted outline. x 1.

VITA.

Olen Forrest Shreve was born at Easton, Maryland in 1878; received his early education at the Friend's Select School, Easton, the Easton High School and the George School, Newtown, Pennsylvania. He received the degree of Bachelor of Arts at the Johns Hopkins University in 1901, entering the graduate department in the same year. His subjects have been Botany, Zoology and Physical Chemistry. He was holder of a University Fellowship in 1904-5.